Depletion of macro-nutrients from rhizosphere soil solution by juvenile corn, cottonwood, and switchgrass plants

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Abstract

In situ sampling of rhizosphere solution chemistry is an important step in improving our understanding of soil solution nutrient dynamics. Improved understanding will enhance our ability to model nutrient dynamics and on a broader scale, to develop effective buffers to minimize nutrient movement to surface waters. However, only limited attention has been focused on the spatial heterogeneity and temporal dynamics of rhizosphere solution, and still less is known about how rhizosphere solution chemistry varies among plant species. Nutrients in rhizosphere soil solution and changes in root morphology of juvenile corn (*Zea mays* L. cv. Stine 2250), cottonwood (*Populus deltoids* L.), and switchgrass (*Panicum virgatum* L.) were monitored using mini-rhizotron technology. Plants were grown for 10 days in a fine-silty, mixed, superactive, mesic Cumulic Hapludoll (Kennebec series). Micro-samples (100–200 μL) of rhizosphere and bulk soil solution were collected at 24-h intervals at a tension of -100 kPa and analyzed for P, K, Ca, and Mg concentration using Capillary Electrophoresis techniques. Plants were harvested at the end of the 10-day period, and tissue digests analyzed for nutrient content by Inductively Coupled Plasma Spectroscopy. Corn plants produced roots that were 1.3 times longer than those of cottonwood, and 11.7 times longer than those of switchgrass. Similar trends were observed in number of root tips and root surface area. At the end of 10 days, rhizosphere solution P and K concentrations in the immediate vicinity of the roots (<1 mm) decreased by approximating 24 and 8% for corn, and 15 and 5% for cottonwood. A rhizosphere effect was not found for switchgrass. After correction for initial plant nutrient content, corn shoot P, K, and Mg were respectively 385, 132, and 163% higher than cottonwood and 66, 37, and 10% higher than switchgrass. Cottonwood shoot Ca concentration, however, was 68 to 133% higher than that of corn or switchgrass. There was no difference in root P concentration among the three species. Nutrient accumulation efficiency (μg nutrient mm^{-1} root length) of cottonwood was 26 to 242% higher for P, 25 to 325% higher for Ca, and 41 to 253% higher for Mg than those of corn and switchgrass. However, K accumulation efficiency of corn was four to five times higher than that of the cottonwood and switchgrass. Nutrient utilization efficiency (mg of dry weight produced per mg nutrient uptake) of P, K, and Mg was higher in cottonwood than in corn and switchgrass. These differences are element-specific and depend on root production and morphology as well as plant nutrient status. From a practical perspective, the results of this study indicate that potentially significant differences in rhizosphere solution chemistry can develop quickly. Results also indicate that cottonwood would be an effective species to slow the loss of nutrients in buffer settings.

Introduction

The rhizosphere is the most chemically and biologically, active micro site in the soil and its ecological

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importance is widely recognized (Toal et al., 2000). Chemical conditions in the rhizosphere can be very different from those of the bulk soil due to root exudation, nutrient uptake, microbial activity, and differences in water relations (Benizri et al., 1997;

Cheng, 2003; Darrah, 1993; Marschner, 1995). Thus, knowledge of rhizosphere chemistry and rhizosphere processes is essential for characterizing nutrient availability in soils. In the last decade, much progress has been made toward a better understanding of the role of rhizosphere processes in plant nutrition, particularly the root-mediated changes in the chemical, physical, and biological properties of the rhizosphere soil (Darrah, 1993; Gregory and Hinsinger, 1999). For example, the role of root hairs and mycorrhizae (Benizri et al., 1997), soil pH changes (Wollenweber, 1997), chelate production (Jones et al., 1996), production of enzymes by roots and bacteria leading to P mineralization (Cheng, 2003; Tarafdar and Jungk, 1987), and the physiological properties of root membranes (Cakmak and Marschner, 1988; Hamza, et al., 2001) are now better understood. However, little attention has been given to the problem of spatial heterogeneity and temporal dynamics of rhizosphere solution, and little is known about the influence of different plant species on rhizosphere solution chemistry. Recent advances in soil solution sampling procedures at the microscale (Göttlein et al., 1996; Wang et al., 2001) and in the analysis of micro-volume solution samples (Göttlein and Blasek, 1996) provide the means to overcome these problems. Improved understanding of rhizosphere solution chemistry will enhance our ability to model nutrient dynamics and to develop on a broader scale, effective buffers to minimize nutrient movement to surface waters.

Using a mini-rhizotron approach, our objective was to evaluate the short-term effect of root activity on rhizosphere solution P, K, Ca, and Mg concentration and compare these changes to the nutrient status of juvenile corn, cottonwood, and switchgrass plants over a 10-day study period. These plant species were chosen for study because they are typical crop and riparian buffer species. This study was conducted in support of a larger project designed to improve our understanding of nutrient movement from cropland through riparian buffers to surface waters.

Materials and methods

Mini-rhizotrons of the type described by Göttlein et al. (1996) were used to conduct the study. The mini-rhizotrons used in this study were 330 mm long, 115 mm wide and 22 mm deep. Each mini-rhizotron was divided into two rectangular chambers, each with a useable volume of 333,000 mm^3. One side of the mini-rhizotron was equipped with a 5×5 mm grid of 1 mm holes for installation of micro suction cups. The opposite side of the mini-rhizotron was equipped with a clear Plexiglas[®] plate to allow the developing roots to be seen. The mini-rhizotron was positioned at an angle of 30° to force the roots to grow toward the Plexiglas[®] plate. The micro suction cups were inserted through the grid on the upper side of the mini-rhizotron and pushed toward the transparent Plexiglas[®] plate.

The micro suction cups were ceramic P80 material with a porosity of 48 vol %, and a maximum pore size of 1 μm (KPM, Berlin, Germany). The cup was glued to a 50 mm length of 1.59 mm polyetheretherketone (PEEK) tubing (inside diameter 0.75 mm). To install the micro suction cups into the soil, a steel scoop having the same dimensions as the micro suction cups was inserted into the soil to the desired depth and then removed. To avoid concentration gradients caused by irrigation, the rhizotron was irrigated with a solution having an ionic composition similar to the equilibrium soil solution. The solution was obtained from a batch soil-water equilibration (soil-water ratio 1: 3 w/w) using procedures described in Wang et al. (2001).

Corn (*Zea mays* L. cv Stine 2250) plants, each having individual root lengths of 20 mm were transplanted into the mini-rhizotrons at the two-leaf stage. The cottonwood (*Populus deltoides* L.) plants were developed from 2-cm greenwood cuttings and roots were trimmed to 20 mm at the time of transplanting. Switchgrass (*Panicum virgatum* L.) plants were started from seed germinated directly in the mini-rhizotron soil. Each of the two chambers in the mini-rhizotron contained 2 corn or 2 cottonwood plants, while each chamber of switchgrass contained 20 plants. After 10 days of growth in the mini-rhizotron, all plants were harvested. We used three mini-rhizotrons, each containing 2 chambers, for a total of 6 replicates per species for the basic experimental setup. All plants were grown in a controlled-environment chamber. Relative humidity in the chamber was maintained at 80%, and the day/night (14 h/10 h) temperature was 25/20 °C. Light intensity was set at 120 μmol m^{-2} s^{-1}.

For each root system, a grid of 15 micro suction cups was installed in front of a developing root system in each chamber of the mini-rhizotron for a total of 30 micro suction cups per mini-rhizotron. As the root system began to develop, the sampling grid was established in the upper half of the chamber in the

anticipated path of the roots. By the end of the study period, approximately 50% of the root system was located in the bounds of the sampling grid. This grid remained in its initial position throughout the study period. The micro suction cups were connected to a vacuum collection box, which allowed the solution from each micro suction cup to be collected in an individual sample vial (Göttlein et al., 1996). The micro suction cups were sampled continuously under a vacuum of −100 kPa and samples were collected at 24-h intervals for 10 days. A computer-regulated vacuum pump attached to the vacuum box maintained a constant −100 kPa tension. The volume collected from each micro suction cup in a 24-h interval was typically in the range of 100–200 μL.

Each chamber of the mini-rhizotron was filled with 260 g of homogenized soil from the B horizon (0.5–1 m) of a fine-silty, mixed, superactive, mesic Cumulic Hapludoll (Kennebec series) collected at the USDA-ARS Deep Loess Research Station located near Treynor, Iowa. Soil was air dried and sieved (< 2 mm) before being placed in the mini-rhizotrons at a bulk density of 1.27 g cm^3. The soil had a pH in water (1: 2.5 w/w soil to water ratio) of 7.68 and solid phase (McGrath and Cunliffe, 1985) total P, K, Ca, and Mg concentrations of 62, 211, 3753 and 474 mg kg^{-1}, respectively. B horizon soil was used in this experiment to avoid any effects from the large volume of dormant seed typically found in the A horizon and to avoid artifacts that the use of soil sterilization to prevent seed germination might have on solution P, K, Ca, and Mg.

Solution samples were analyzed by Capillary Electrophoresis using a P/CE System MDQ from Beckman (Fullerton, CA, USA). Phosphorus was measured using a buffer solution consisting of 8 mM Tris (hydroxymethyl) aminomethane (TRIS) (99.9%), 2 mM 1,2,4-benzenetricarboxylic [(trimellitic acid) (TMA)] (99%) and 0.3 mM tetradecyltrimethylammonium bromide (TTAB) (99%) at a pH of 7.6 (Westergaard et al., 1998). Separations were performed in a fused-silica capillary of 75 μm id (Beckman, Fullerton, CA, USA) and an applied separation voltage of −30 kv at a temperature of 20 °C and a detection wavelength of 254 nm. Pretreatment of the capillary between each run included rinsing with a 0.1 M sodium hydroxide solution for 1 min, deionized water for 0.5 min, followed by preconditioning with the electrolyte for 5 min. For the analysis of K, Ca, and Mg, we used a buffer system consisting of 5 mM Metol, 1mM Ascorbic, and 2 mM 18-Crown-6. Separation was done at 20 °C with +30 kV voltage at a detection wavelength of 220 nm (Wang et al., 2001).

At the end of 10 days, root length, root surface area, and number of root tips of six plants of each species were determined using Rootedge software (Kaspar and Ewig, 1997). For nutrient analysis, all plants growing in a microcosm were harvested and combined into a single sample for that microcosm. Plant samples were oven dried at 65 °C, milled, and digested with HCl : HNO$_3$ (4:1) and analyzed for P, K, Ca, and Mg by ICP-AES using procedures described by McGrath and Cunliffe (1985). Nutrient-accumulation efficiency (ratio of total nutrient accumulated to total root length) and nutrient-utilization efficiency (ratio of produced biomass to unit of nutrient uptake) (Fageria, 1992) were calculated. Uptake values calculated at the end of the study were adjusted for initial plant or seed nutrient content.

To simplify data presentation and enable a comparison of the different micro suction cup matrices, the sampling events were classified according to day number, with the first day that a root entered the micro suction cup grid assigned as day 0. Distance from a suction cup to the root was classified as being in one of three classes: <1 mm, 1–8 mm, >8 mm, depending on the location of the sampling point relative to the root. Previous evaluation (Wang et al., 2004) indicated that grouping sampling points into these three distance categories would provide enough data points in each category for statistical analysis. Mean concentration values for P, K, Ca, and Mg were obtained by averaging all values with the same day number and the same distance class. The distance based approach leads to a variable number of samples on each sampling day as root proximity within the sampling grid changed due to root growth.

Analysis of variance (SPSS Version 11.0) was used to test the main effect of species on solution nutrient concentrations, root parameters, and seedling nutrient concentrations. The differences between mean values were verified by One-Way ANOVA, and Duncan's test was used to separate treatment means exhibiting significant differences. The number of observations used in the statistical analyses varied with the parameter being evaluated.

Results

As might be anticipated, shoot and root biomass differed among corn, cottonwood, and switchgrass plants

(Table 1). Corn had the lowest shoot/root (g/g) ratio (0.53) when compared to cottonwood (2.28) and switchgrass (2.14) (Table 1). Length of the roots for the three species varied from 305 to 3869 mm, the number of root tips varied between 136 and 1385, and root surface area varied from 77 to 1873 mm^2 (Table 1). After 10 days of growth, corn roots were 1.3 times longer than the roots of cottonwood and 11.7 times longer than the roots of switchgrass. Similar trends were observed for the number of root tips and root surface area (Table 1).

For corn, solution concentrations of P and K were lower in close proximity to roots compared to solution collected at >8 mm from the root in what might be considered the bulk soil (Figures 1 and 2). For corn, a decreasing P concentration was found after only 5 days at both the 0–1 and 1–8 mm ranges. Values at these two distances were 22 and 13%, respectively, lower than the values from the >8 mm distance. By the end of 10 days, P concentration at the 0-1 and 1-8 mm sampling points were 76 to 78% of those observed at >8 mm, separately. Potassium concentration in the 0–1 mm range of corn plants was about 92% of those at >8 mm at 10 days. However, there were no differences in K concentration at the 1–8 and >8 mm sampling points at the end of 10 days.

For cottonwood, there were no differences in P or K concentration as a function of distance at the end of 5 days. By day 10 however, P concentration decreased by 15% more in the 0–1 mm range than in the 1–8 and >8 mm ranges. At the end of 10 days, cottonwood K concentrations at all distances from the roots had not changed (Figure 2).

No differences in Ca or Mg concentration were found at any distance from the roots of corn or cottonwood. Nor was there any rhizosphere effect on P, K, Ca, or Mg concentrations observed near the roots of switchgrass (Table 2).

Tissue P, K, Ca, and Mg concentrations differed (p<0.05) for the three species under study (Table 3). Corn shoot P, K, and Mg concentrations were 10 to 485% higher compared to switchgrass and cottonwood. The cottonwood shoot Ca concentration, however, was 68 to 133% higher than those of corn and switchgrass. There was no difference in root P concentration among corn, cottonwood, and switchgrass. By contrast, the root Mg concentration was 20% less in corn than in switchgrass and cottonwood while K concentration was approximately 300% higher. Root Ca concentration differed by species with corn having the highest and switchgrass the lowest (Table 3).
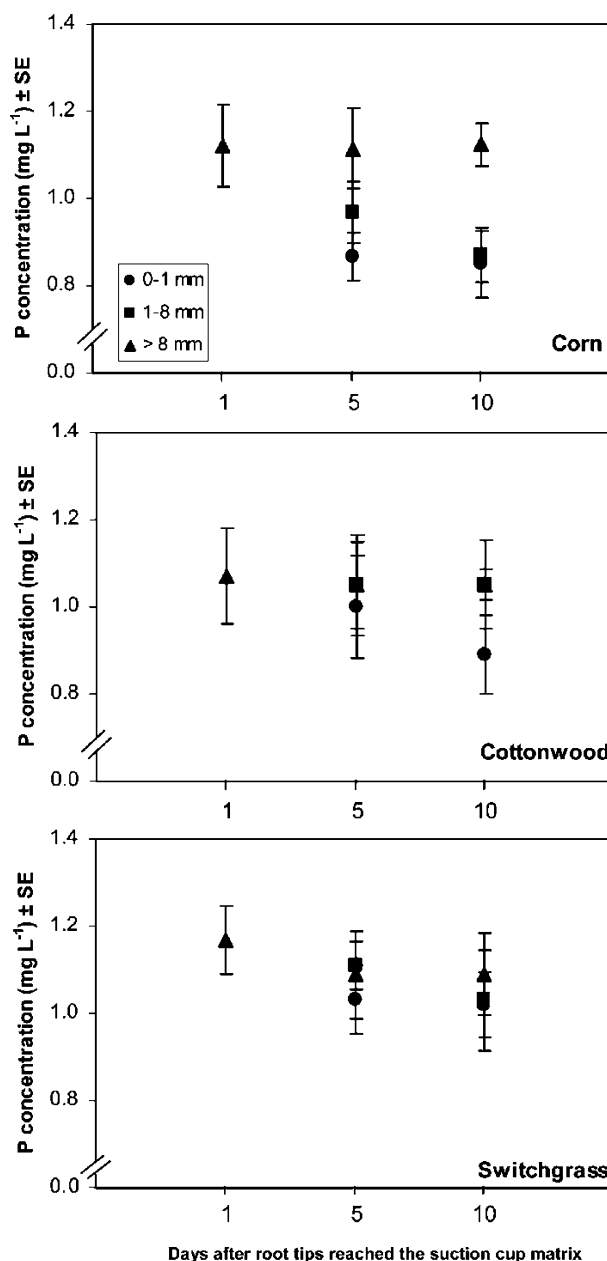

Figure 1. Mean phosphorus concentration in the soil solution for three different root distance classes after10 days for corn, cottonwood, and switchgrass plants. Bars in each figure are the mean and standard error of all sampling points falling within a particular distance class at 10 days. The number of sampling points within each distance class can change with sample day. Letters above the bars indicate means within a species that were statistically different at $P = 0.05$.

Nutrient-accumulation efficiency of the cottonwood was 26 to 242% higher for P, 25 to 352% higher for Ca, and 41 to 253% higher for Mg than those of
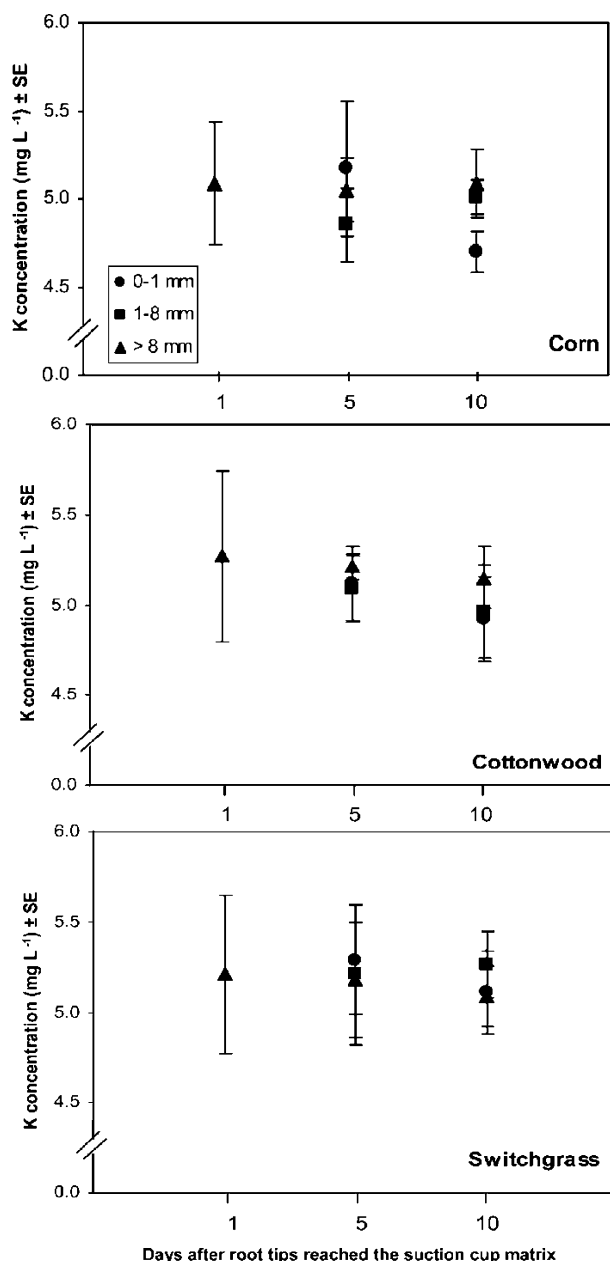
Figure 2. Mean potassium concentration in the soil solution for three different root distance classes after 10 days for corn, cottonwood, and switchgrass plants. Bars in each figure are the mean and standard error of all sampling points falling within a particular distance class at 10 days. The number of sampling points within each distance class can change with sample day. Letters above the bars indicate means within a species that were statistically different at $P = 0.05$.

the corn and switchgrass. However, K accumulation efficiency of corn was four to five times higher than that of cottonwood or switchgrass (Figure 3).

Compared to the nutrient-utilization efficiency of cottonwood, corn and switchgrass were 63 and 48% less efficient for P, 61 and 15% less efficient for K, and 19 and 26% less efficient for Mg (Figure 4). However, the Ca utilization efficiency of switchgrass was 44% higher than that of corn, and 130% higher than that of cottonwood.

Discussion

George and Marschner (1996), as well as many others, have demonstrated that root systems of various plant species differ in both root morphology and physiology. Differences in root biomass and root morphology frequently lead to differences in nutrient uptake due either to improved proximity to nutrients, as is the case with a large root system, or more efficient physiological processes, as in the case of higher rates of nutrient uptake per unit of root (Rao, et al. 1997; Wang et al., 2001, 2003). These differences in root system morphology among various plant species have been shown to influence soil solution chemistry in the vicinity of the root (Jungk and Claassen, 1986; Marschner, 1995; Wang et al., 2001, 2003) through differences in acquisition of nutrients and water. When roots intensively ramify a particular volume of soil, the potential to create a more uniform chemical environment is greater. This is due in part to the shorter distances between roots leading to reduced diffusion and transport distances for various nutrients. Greater distances between root axes can lead to a more heterogeneous pattern in the soil due to various segments of the soil being more or less impacted by the presence or absence of root influences. Our results are consistent with these hypotheses in that corn and cottonwood with more root length and root tips (Table 1) had the potential to modify soil chemistry more than the less developed switchgrass root system. Our results also suggest that corn acquires more of its nutrients by soil exploration, while cottonwood exploits its rhizosphere more efficiently.

Rhizosphere soil solution is expected to be more responsive to changes caused by root-soil interactions than rhizosphere soil because soil solution is the medium for soil chemical exchange and biochemical reactions. Data presented in Table 2 clearly illustrate a difference in solution P concentration in the rhizosphere of corn and cottonwood when compared to bulk soil. It is quite likely that diffusion plays an important role in the delivery of P and K to these roots
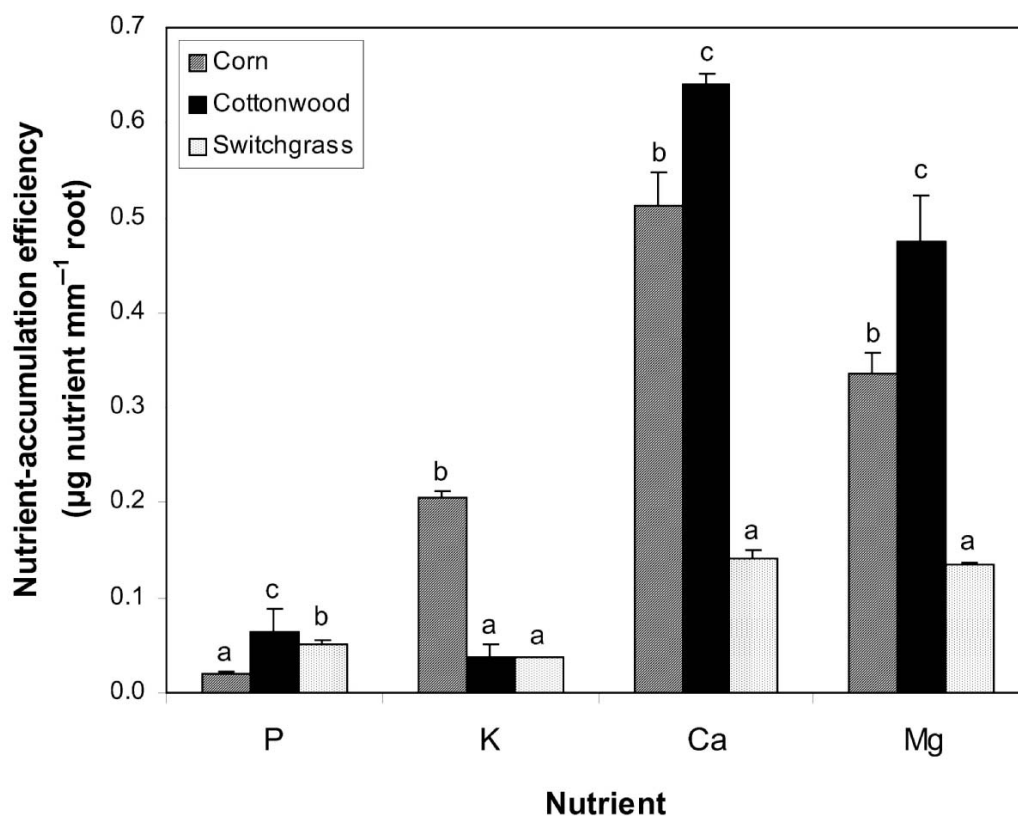
Figure 3. Whole plant nutrient-accumulation efficiency (ratio of total accumulated nutrient to total root length) for corn, cottonwood, and switchgrass plants grown for 10 days in a controlled environment mini-rhizotron study. Letters above the bars indicate means that were statistically different at $P = 0.05$.

(Hylander et al., 1999; Marchner, 1995) and the relatively larger mass of the growing corn and cottonwood plants created a much greater demand for these nutrients than occurred for the relatively small switchgrass plants.

In contrast to the P and K response, Ca and Mg concentrations at the end of 10 days of growth did not change as a function of distance from the root (Table 2). Whether or not a nutrient gradient will form in the rhizosphere depends on many factors including the current nutrient status of the plant (Marschner, 1995) and the ability of the soil solid phase to sustain the solution phase concentration (Barber, 1995). For example, Barber and Ozanne (1970) used an autoradiographic technique to determine that while ryegrass, subclover, and capeweed experienced an accumulation of Ca around the root, Ca in the rhizosphere of lupin was depleted. In the former case, mass flow delivered Ca to the root at a rate sufficient to offset uptake, while in the latter, soil supply was not adequate to keep up with plant demand. In our case, it would appear that

mass flow supported by a relatively high soil solid phase supply was sufficient to buffer any potential changes created by Ca and Mg uptake. This hypothesis is supported by the observations of Marschner et al. (1991) and Bakker et al. (1999) that at a soil solution concentration of 5 mg Ca L^{-1}, mass flow transported Ca was sufficient to meet the required Ca uptake by the roots of forest trees. Similarly, Seggewiss (1986) studied Mg distribution in the rhizosphere of rape plants and found that depending on the soil exchangeable Mg level, exchangeable Mg in the rhizosphere could be accumulated (> 444 mg L^{-1}), depleted (<43 mg L^{-1}) or remain unchanged (117 mg L^{-1}) which may be taken as an indication of the relative balance between the soil delivery rate and plant demand.

Our results confirm that the development of a nutrient gradient in the rhizosphere is related to differences among plant species and the type of nutrient (Figures 1 and 2; Table 2). Compared to bulk solution, rhizosphere solution P and K concentrations in the corn mini-rhizotrons decreased by 24% and 8%, respec-
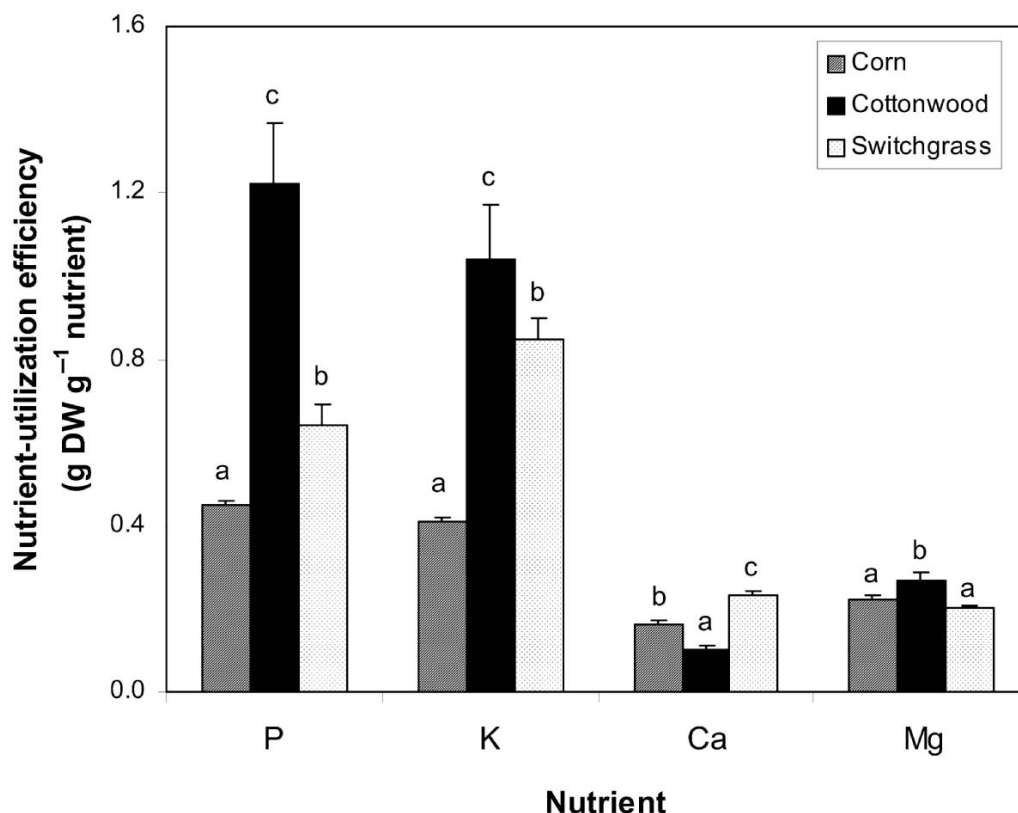
Figure 4. Whole plant nutrient-utilization efficiency (ratio of produced biomass to invested nutrient) for corn, cottonwood, and switchgrass plants grown for 10 days in a controlled environment mini-rhizotron study. Letters above the bars indicate means that were statistically different at $P = 0.05$.

tively. Phosphorus concentration in the cottonwood rhizosphere decreased by 15%, while K concentration was unchanged. The lack of change in rhizosphere soil solution chemistry for switchgrass is attributed to the fact that the root system of the switchgrass plants had not developed sufficiently to change the chemical environment in the rhizosphere and that any potential change was offset by the influences of diffusion and mass flow. Comparison of root surface area values in Table 1 support this conjecture in that the surface area of switchgrass roots was less than 5% of the corn and cottonwood values. It is also possible, given the size of the switchgrass plants, that a significant plant nutrient demand had not yet developed. These observations point out the need in future comparisons to either use a transplant approach where plants are of similar initial biomass, or alternatively to allow more time for the switchgrass plants and roots to develop. In the case of the latter, this would require the use of a much larger mini-rhizotron to prevent the soil volume from being so densely populated with roots as to make gradient detection impractical.

Various researchers have used either nutrient-use efficiency or nutrient-uptake efficiency as a means to assess the ability of plants to acquire nutrients (Bhadoria et al., 2002; Ciarelli et al., 1998; Fageria and Baligar, 1999). In the present experiment, we found significant species differences in nutrient-utilization and -accumulation efficiency in corn, cottonwood, and switchgrass (Figures 3 and 4). Young cottonwood plants appear to be more efficient accumulators of nutrients than corn and switchgrass, although the comparison with switchgrass is probably not valid due to its lack of adequate root development compared to the other two species. Focusing then on corn and cottonwood, the observed differences may be due to several factors, which may include root morphology, root extension, and biochemical and physiological mechanisms (Jackson et al., 1986). For example, Wang et al. (2003) in a study of beech and spruce seedlings found

that spruce had both a higher nutrient-accumulation and nutrient-use efficiency. Since spruce trees typically grow on less fertile soils than beech, these differences can probably be attributed to a physiological adaptation on the part of spruce to deal with reduced nutrient availability. In contrast, most varieties of corn have been selected for growth in soils with relatively high levels of nutrient supply. Work by Barber and colleagues (Barber, 1995) has shown that nutrient uptake by many crop species will decline significantly or even stop at reduced soil solution concentration levels while uptake of nutrients by woody species will continue until solution nutrient levels near zero (Kelly and Barber, 1991; Kelly and Kelly, 2001). From another perspective, Bhadoria et al. (2002) found that the plant traits that led to the same level of P efficiency were quite different for wheat and sugar beet. Wheat relied on a large root system and low shoot growth rate as a means to keep demand on the root at a level that can be easily satisfied by P influx. In contrast, sugar beet had a high shoot growth rate and only a few roots, putting a high nutrient demand on each root segment. It is also worthwhile to note that cottonwood acquired more nutrients per volume of rhizophere than corn. The subsequent decline in soil solution is less for mobile nutrients like P and occurred later for cottonwood. This might suggest that cottonwood is capable of maintaining the soil nutrient solution equilibrium longer through mechanisms of nutrient mobilization. Based on these observations, data collected in this study, and other reports in the literature, nutrient-uptake and nutrient-use efficiencies are a function of the combined influences of root system morphology, growth, and physiological parameters that will vary with species and possibly with cultivars within a species. These differences can have substantial influence on the formation of rhizosphere nutrient gradients over time.

From a practical perspective, the results of this study indicate that potentially significant differences in rhizosphere solution chemistry develop rather quickly and improved ways of representing these differences are needed if we are to increase the accuracy of mechanistic nutrient uptake and nutrient loss models. Continuing to treat the soil as a homogeneous nutrient supply system may be acceptable or even necessary at the landscape level, but doing so leads to increasing levels of error in many cases as the scale of evaluation is reduced down to the individual plant-soil combination. Likewise, when designing riparian buffer systems it is important to recognize the rela-

tive differences in the ability of various plant species to capture nutrients through root uptake. Cottonwood appears to be an effective species for nutrient capture, but our results for switchgrass are inconclusive. Work should therefore be undertaken to evaluate the timing of nutrient uptake, the rate of uptake, and amount of uptake, as well as total biomass production for these and other species as we seek to refine our recommendations for appropriate plant species to use in the design of riparian buffer systems that are more effective in the capture of a broader suite of nutrients.

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